A review of the diet of flower wasps (Hymenoptera: Thynnidae: Thynninae)

Graham R. Brown[1] and Ryan D. Phillips[2,3]

[1] Museum and Art Gallery of the Northern Territory,
GPO Box 4646, Darwin, NT 0801, Australia. Email: thynnini@hotmail.com
[2] Evolution, Ecology and Genetics, Research School of Biology,
The Australian National University, Canberra, ACT 0200, Australia.
[3] Kings Park and Botanic Garden, The Botanic Garden and Parks Authority,
West Perth, 6005, Western Australia.

Abstract

The feeding preferences of Australian flower wasps (Thynnidae: Thynninae) are reviewed based on the available literature, a search of a specimen database of almost 8,000 records and an examination of selected representatives of all described genera for the presence of pollen. The vast majority of records of feeding by flower wasps are on nectar, but they also feed on the exudates of scale insects, leafhoppers and aphids. The plants visited most frequently are from the family Myrtaceae, with most other families represented by only a small number of records. Interestingly, there are almost no records from several of Australia's most diverse plant families. It remains to be tested if members of the Myrtaceae show specific adaptations to pollination by flower wasps or if there is variation in wasp morphology in response to variation in diet. Future dietary studies of flower wasps should aim to quantify both floral and other food sources to aid in understanding the ecological requirements of these wasps and how they co-exist in such diverse communities.

Introduction

The name 'flower wasp' was first used by Froggatt (1907) in his book *Australian Insects* and it subsequently came into common usage for the entire Australian thynnine wasp fauna (Tillyard 1926; Naumann 1993). Froggatt applied this common name to the family Thynnidae as it was then constituted. Since that time there have been several taxonomic changes to the higher classification of the group (Pate 1947; Brothers 1975; Brothers & Carpenter 1993) such that the Thynnidae of Froggatt is now a subfamily within a wider interpretation of the family Thynnidae (Pilgrim *et al.* 2008). Within the Australian context, the only other change since Froggatt (1907) was the inclusion into the family of the so-called Blue Ant (*Diamma bicolor*). This distinctive species from southeastern Australia was placed at the rank of a subfamily (Diamminae) by Salter (1963), and is still the only member of that subfamily.

Flower wasps vary in size from 3–45 mm in length. They exhibit a pronounced sexual dimorphism. Males are most commonly predominantly black, though they are often brightly patterned, especially with yellow. While the males are strong fliers, with large species capable of flying several hundred metres (Menz *et al.* 2013), females are always smaller, wingless, and somewhat ant-like in appearance. Females are mostly dull orange to black in colour although some, especially the larger species, are marked with yellow. In Australia, there are approximately 600 described species of flower wasps in 48 genera with an estimated 2,000 species currently represented in collections, including many new genera.

Despite representing a diverse component of the Australian wasp fauna, very little is known about the biology of flower wasps. Courtship is initiated by the female releasing pheromones that rapidly attract males (Alcock & Gwynne 1987; Peakall 1990; Peakall *et al.* 2010). Copulation takes place in flight, with the female curled back underneath the abdomen of the male (Alcock & Gwynne 1987). Because female flower wasps are flightless, they are dependent on the male for food during these courtship flights. Provision of food may be by regurgitation and/or by being flown to a food source *in copula*, with the female then allowed to feed while mating continues (Froggatt 1907; Given 1953). Coupling can last up to two days in captivity (Williams 1919). This prolonged coupling and the pronounced sexual dimorphism is unique and distinctive within the Australian wasp fauna, making mating pairs of thynnines easy to recognise. After mating has been completed, the female is dropped on the ground, after which it parasitises subterranean scarab larvae (Williams 1919; Given 1953; Ridsdill Smith 1970a), although other hosts such as ants (Turner 1914; G. Brown, unpubl.) and bees (Rayment 1935) have also been suggested.

Adult males and copulating pairs are commonly observed at flowers feeding on nectar, with an apparent preference for some genera of the family Myrtaceae (Given 1953; Phillips *et al.* 2009). However, large numbers of individuals have also been observed feeding on *Xanthorrhoea* (Xanthorrheaceae) and *Hakea* (Proteaceae), particularly in southwestern Australia (Phillips *et al.* 2009). Thus far, most knowledge of their food plant preferences comes from opportunistic collections rather than systematic studies. A notable exception to these field records is the work of Menz *et al.* (2013), where pollen swabs were used to show that two species of *Zaspilothynnus* appear to feed primarily on Myrtaceae. Even more poorly documented than nectar foraging, is foraging on exudates of insects, for which there is almost no specific documentation of the flower wasp, or insect, or plant species involved.

While the natural history of most flower wasps remains poorly known, there is increasing interest in their biology due to their role as pollinators of some species of terrestrial orchids. These orchids, of which over 200 species are known from Australia, deceive flower wasps into mating with them. Sexually deceptive orchids engage in chemical and physical mimicry of the calling female, with pollination achieved as the male attempts pre-mating or copulatory behaviour with the flower

(Peakall 1990). As a by-product of mimicking the specific sex pheromones of insects, these orchids have highly specialised pollination systems, typically relying on just a single pollinator species. This reliance on a single pollinator may be a major contributor to the trend of greater rarity in sexually deceptive orchids (Phillips *et al.* 2011), thus highlighting the importance of understanding the ecological requirements of pollinators for plant conservation.

Given the increasing recognition of both the diversity of flower wasps and their role as pollinators, it is pertinent to synthesise current knowledge on their diet. We review the known literature on food plants, use collection details from a nationwide database of specimens and examine museum specimens for the presence of pollen. Combining these approaches represents the first step in understanding the dietary breadth of flower wasps, in investigating if there are generic differences in food plants, and testing if there is an association between diet and mouthpart morphology. This paper is intended as an introduction to further studies on the relationship between flower wasp abundance, their dietary requirements and their effectiveness as pollinators of orchids that attract pollinators through sexual deceit.

Materials and Methods

A search was made for records of flower wasps feeding on flowers and other foods. It involved a literature search including all original species descriptions, an examination of representative specimens from all Australian genera for the presence of pollen, and a search of a personal (GRB) research database containing nearly 8,000 records.

It was assumed that all references to host plants on data labels referred to the flowers unless specified otherwise. The only exception was the genus *Acacia*, which has extra-floral nectaries at the base of the leaves rather than nectar-rich flowers (Bernhardt 1987). For all discussions, we have only gone to the level of plant and wasp genus, as there is currently insufficient data to draw trends at the species level.

Pinned male specimens were examined for the presence of pollen, plus its abundance and distribution, for a comparison of wasp genera. Females were not examined as they were collected *in copula*, walking on the ground or attracting males with pheromones. It is likely that such females had recently emerged from below the ground. As females spend most of their time below the surface seeking hosts to parasitise, it is likely that any pollen present would soon be abraded away. Data were not quantified other than to record whether pollen could be found on representative wasps of all described genera. Observations were based on specimens available in Darwin in August 2013, whether in local collections or on loan from other institutions at that time (Australian Museum, Sydney; Museum of Victoria, Melbourne; Queensland Museum, Brisbane; South Australian Museum, Adelaide; Western Australian Museum, Perth). No attempt was made to identify pollen grains.

Results

Literature Survey

Most published host records of the food plants of flower wasps are for myrtaceous flowers (Tillyard 1926). Within the Myrtaceae, flower wasps have been recorded feeding on flowers of the genera *Eucalyptus* (Burrell 1935; Salter, 1967; Ridsdill Smith 1970b; Alcock 1981; Phillips *et al.* 2009; Menz *et al.* 2013), *Leptospermum* (Bridwell 1917; Burrell 1935; Given 1953; Ridsdill Smith 1970b; Alcock 1981; Alcock & Gwynne 1987; Phillips *et al.* 2009), *Angophora* (Bridwell 1917; Salter 1967), *Melaleuca* (Burrell 1935), *Chamelaucium* (Alcock & Gwynne 1987; Phillips *et al.* 2009) and *Agonis* (Menz *et al.* 2013). Most of these genera produce nectar-rich flowers (Goodacre 1947). Outside the Myrtaceae, large aggregations of feeding flower wasps have been observed on the flowers of *Hakea* (Proteaceae) (Given 1953; Phillips *et al.* 2009) and *Xanthorrhoea* (Xanthorrhoeaceae) (Phillips *et al.* 2009).

Campbell & Brown (1998) intensively sampled flower wasps and other parasites of scarab larvae at two locations on the Northern Tablelands of New South Wales. Almost all observations of feeding were made from myrtaceous flowers of the genera *Baeckea* and *Leptospermum*. *Kunzea* was unattractive, while *Eucalyptus* did not flower during the study due to a prolonged drought.

During a study of the pollination biology of several species of *Acacia* from southeastern Australia, Bernhardt (1987) observed members of the flower wasp genera *Lophocheilus*, *Phymatothynnus*, *Rhagigaster* and *Tachynomyia* feeding on extra-floral nectaries and the nectarless flowers.

Burrell (1935) gave several food plant records for individual wasp genera: *Thynnus* from *Leptospermum* and *Eucalyptus*; *Dimorphothynnus*, *Catocheilus* and *Lophocheilus* from *Eucalyptus*; and *Eirone*, *Neozeleboria*, *Rhagigaster*, *Thynnoides* and *Zeleboria* on the exudates of scale insects (Coccoidea). While thynnines have been observed feeding on the exudates of scale insects (Burrell 1935; Given 1953; Schiestl 2004), leafhoppers (Ridsdill Smith 1970b) and aphids (Given 1953), there are comparatively few records of this behaviour.

Of particular interest is an insightful paper by Given (1957), in which he speculates on different feeding habits, including regurgitation, in relation to modifications to the head shape and mouthparts. This possibility is further discussed by Ridsdill Smith (1970a, 1970b). It should be noted however, that neither author gives quantitative data, making it possible to overestimate the importance of regurgitation without studying this in the broader context of individual feeding strategies.

Additional general observations are given by Illingworth (1921), Given (1953, 1957), Ridsdill-Smith (1970b, 1971), Campbell & Brown (1994) and Brown *et al.*, (1997).

Data labels/Database

Using specimen label data from Australian museums, we compiled records of 39 wasp genera visiting 33 plant genera, representing 14 families (i.e. 121 wasp by plant genus records). Of these, 77 (64%) are from Myrtaceae from 14 genera (Table 1). However, it should be noted that only a small number of specimens examined have host records or collecting methods included on their data labels. The plant genera on which the greatest range of wasp genera have been recorded feeding are *Eucalyptus* (20 genera of flower wasps), *Leptospermum* (9 genera), *Melaleuca* (9 genera) and *Chamelaucium* (9 genera). Of the genera outside the Myrtaceae, the highest numbers of records are from *Hakea* (Proteaceae), with almost all of these from species with cream-coloured flowers from Western Australia. The authors have observed previously that thynnines may be abundant on the flowers of *Bursaria* (Pittosporaceae), *Vigna* (Fabaceae) (grown as legume crops), and *Xanthorrhoea* (Xanthorrhoeaceae).

Table 1. Records of food plants (at the level of genus) for genera of flower wasps based on label data for specimens in Australian museum collections.

FLOWER FAMILY	FLOWER GENUS	WASP GENUS
Amaranthaceae	*Rhagodia*	*Agriomyia*
Amaranthaceae	*Rhagodia*	*Aspidothynnus*
Fabaceae	*Vigna*	*Epactiothynnus*
Fabaceae	*Vigna*	*Umbothynnus*
Goodeniaceae	*Scaevola*	*Acanthothynnus*
Goodeniaceae	*Scaevola*	*Agriomyia*
Goodeniaceae	*Scaevola*	*Zeleboria*
Gyrostemonaceae	*Codonocarpus*	*Encopothynnus*
Lamiaceae	*Pityrodia*	*Guerinius*
Lamiaceae	*Prostanthera*	*Lestricothynnus*
Myrtaceae	*Agonis*	*Zaspilothynnus*
Myrtaceae	*Angophora*	*Aspidothynnus*
Myrtaceae	*Angophora*	*Doratithynnus*
Myrtaceae	*Astartea*	*Elidothynnus*
Myrtaceae	*Astartea*	*Thynnoides*
Myrtaceae	*Astartea*	*Zaspilothynnus*
Myrtaceae	*Baekea*	*Elidothynnus*
Myrtaceae	*Callistemon*	*Tachynomyia*
Myrtaceae	*Chamelaucium*	*Aulacothynnus*
Myrtaceae	*Chamelaucium*	*Catocheilus*
Myrtaceae	*Chamelaucium*	*Macrothynnus*
Myrtaceae	*Chamelaucium*	*Megalothynnus*
Myrtaceae	*Chamelaucium*	*Rhagigaster*
Myrtaceae	*Chamelaucium*	*Zaspilothynnus*
Myrtaceae	*Chamelaucium*	*Zeleboria*
Myrtaceae	*Corymbia*	*Agriomyia*
Myrtaceae	*Corymbia*	*Zaspilothynnus*

(continued)

Table 1. Continued.

FLOWER FAMILY	FLOWER GENUS	WASP GENUS
Myrtaceae	*Eucalyptus*	*Agriomyia*
Myrtaceae	*Eucalyptus*	*Arthrothynnus*
Myrtaceae	*Eucalyptus*	*Aspidothynnus*
Myrtaceae	*Eucalyptus*	*Aulacothynnus*
Myrtaceae	*Eucalyptus*	*Beithynnus*
Myrtaceae	*Eucalyptus*	*Caetrathynnus*
Myrtaceae	*Eucalyptus*	*Campylothynnus*
Myrtaceae	*Eucalyptus*	*Catocheilus*
Myrtaceae	*Eucalyptus*	*Curvothynnus*
Myrtaceae	*Eucalyptus*	*Doratithynnus*
Myrtaceae	*Eucalyptus*	*Elidothynnus*
Myrtaceae	*Eucalyptus*	*Encopothynnus*
Myrtaceae	*Eucalyptus*	*Guerinius*
Myrtaceae	*Eucalyptus*	*Iswaroides*
Myrtaceae	*Eucalyptus*	*Procerothynnus*
Myrtaceae	*Eucalyptus*	*Rhagigaster*
Myrtaceae	*Eucalyptus*	*Rhytidothynnus*
Myrtaceae	*Eucalyptus*	*Thynnoides*
Myrtaceae	*Eucalyptus*	*Zaspilothynnus*
Myrtaceae	*Eucalyptus*	*Zeleboria*
Myrtaceae	*Kunzea*	*Catocheilus*
Myrtaceae	*Leptospermum*	*Arthrothynnus*
Myrtaceae	*Leptospermum*	*Aspidothynnus*
Myrtaceae	*Leptospermum*	*Campylothynnus*
Myrtaceae	*Leptospermum*	*Dimorphorphothynnus*
Myrtaceae	*Leptospermum*	*Doratithynnus*
Myrtaceae	*Leptospermum*	*Eirone*
Myrtaceae	*Leptospermum*	*Elidothynnus*
Myrtaceae	*Leptospermum*	*Lestricothynnus*
Myrtaceae	*Leptospermum*	*Lophocheilus*
Myrtaceae	*Leptospermum*	*Megalothynnus*
Myrtaceae	*Leptospermum*	*Neozeleboria*
Myrtaceae	*Leptospermum*	*Oncorhinothynnus*
Myrtaceae	*Leptospermum*	*Phymatothynnus*
Myrtaceae	*Leptospermum*	*Rhytidothynnus*
Myrtaceae	*Leptospermum*	*Rhytidothynnus*
Myrtaceae	*Leptospermum*	*Thynnoides*
Myrtaceae	*Leptospermum*	*Tmesothynnus*
Myrtaceae	*Leptospermum*	*Zaspilothynnus*
Myrtaceae	*Leptospermum*	*Zeleboria*
Myrtaceae	*Melaleuca*	*Agriomyia*
Myrtaceae	*Melaleuca*	*Aspidothynnus*
Myrtaceae	*Melaleuca*	*Doratithynnus*

(continued)

Table 1. Continued.

FLOWER FAMILY	FLOWER GENUS	WASP GENUS
Myrtaceae	*Melaleuca*	*Elidothynnus*
Myrtaceae	*Melaleuca*	*Guerinius*
Myrtaceae	*Melaleuca*	*Iswaroides*
Myrtaceae	*Melaleuca*	*Macrothynnus*
Myrtaceae	*Melaleuca*	*Procerothynnus*
Myrtaceae	*Melaleuca*	*Rhagigaster*
Myrtaceae	unidentified	*Psammothynnus*
Myrtaceae	*Scholtzia*	*Guerinius*
Myrtaceae	*Scholtzia*	*Lophocheilus*
Myrtaceae	*Scholtzia*	*Rhagigaster*
Myrtaceae	*Scholtzia*	*Zaspilothynnus*
Myrtaceae	*Verticordia*	*Belothynnus*
Myrtaceae	*Verticordia*	*Catocheilus*
Myrtaceae	*Verticordia*	*Oncorhinothynnus*
Myrtaceae	*Verticordia*	*Zaspilothynnus*
Orchidaceae	*Prasophyllum*	*Dimorphorphothynnus*
Orchidaceae	*Prasophyllum*	*Eirone*
Orchidaceae	*Prasophyllum*	*Rhagigaster*
Orchidaceae	*Prasophyllum*	*Rhytidothynnus*
Orchidaceae	*Prasophyllum*	*Zaspilothynnus*
Pittosporaceae	*Bursaria*	*Agriomyia*
Pittosporaceae	*Bursaria*	*Arthrothynnus*
Pittosporaceae	*Bursaria*	*Guerinius*
Proteaceae	*Adenanthos*	*Elidothynnus*
Proteaceae	*Banksia*	*Catocheilus*
Proteaceae	*Hakea*	*Aspidothynnus*
Proteaceae	*Hakea*	*Campylothynnus*
Proteaceae	*Hakea*	*Catocheilus*
Proteaceae	*Hakea*	*Dimorphorphothynnus*
Proteaceae	*Hakea*	*Doratithynnus*
Proteaceae	*Hakea*	*Macrothynnus*
Proteaceae	*Hakea*	*Rhagigaster*
Proteaceae	*Hakea*	*Thynnoides*
Proteaceae	*Hakea*	*Zaspilothynnus*
Proteaceae	*Lambertia*	*Aspidothynnus*
Sapindaceae	*Alectryon* (as *Heterodendrum*)	*Encopothynnus*
Sapindaceae	*Atalaya*	*Aspidothynnus*
Sapindaceae	*Atalaya*	*Doratithynnus*
Scrophulariaceae	*Eremophila*	*Aspidothynnus*
Scrophulariaceae	*Eremophila*	*Dimorphorphothynnus*
Thymelaeaceae	*Pimelea*	*Agriomyia*
Thymelaeaceae	*Pimelea*	*Guerinius*
Thymelaeaceae	*Thryptomene*	*Aspidothynnus*

(continued)

Table 1. Continued.

FLOWER FAMILY	FLOWER GENUS	WASP GENUS
Xanthorrhoeaceae	*Xanthorrhoea*	*Catocheilus*
Xanthorrhoeaceae	*Xanthorrhoea*	*Doratithynnus*
Xanthorrhoeaceae	*Xanthorrhoea*	*Macrothynnus*
Xanthorrhoeaceae	*Xanthorrhoea*	*Zaspilothynnus*

All wasp genera for which there were more than five host genera records (i.e. *Agriomyia, Aspidothynnus, Catocheilus, Elidothynnus, Guerinius, Rhagigaster, Rhytidothynnus, Thynnoides* and *Zaspilothynnus*) have been found on several families of plants including the Myrtaceae. All genera with host records had at least one record from the Myrtaceae except for two: *Acanthothynnus* with one record from *Scaevola* (Goodeniaceae) and *Umbothynnus* with one record (but multiple specimens) on *Vigna* (Fabaceae). Both genera are small and poorly represented in collections.

Of the non-flower records, five wasp genera (i.e. *Aspidothynnus, Doratithynnus, Encopothynnus, Iswaroides* and *Rhytidothynnus*) were recorded from *Acacia* (Fabaceae), where they were most likely feeding on extra-floral nectaries rather than flowers. There were also records of *Neozeleboria* trapped in the sticky seeds of *Pisonia brunoniana* (Nyctaginaceae) and *Eirone* feeding on exudates of the soft scales *Eriococcus coriaceus* (Coccidae).

There were no host label data records for the wasp genera *Aeolothynnus, Ariphron, Bifidothynnus, Chilothynnus, Dythynnus, Gymnothynnus, Leiothynnus, Nitidothynnus, Pentazeleboria, Tachynoides, Tachyphron* or *Thynnus* on the specimens examined.

Examination of specimens

Pollen was found on many specimens and most genera. While some individuals had a dense covering of pollen, most had only a few grains that were retained in depressions or grooves (but not punctures) particularly at the base of the antennae, the anterior transverse groove on the pronotum and at the base of the wings (but not in cavities in the fore coxae). Those specimens that had a heavy pollen load did have some pollen on the setae. Wasps frequently preen themselves and such specimens were probably caught on flowers before they had time to remove much of the pollen.

Pollen was usually found on the integument, but not attached to the setae themselves (Figures 1, 2), although the setae may help to hold some grains in place. All setae arise from punctures in the integument so that the densities of the setae and the punctures are identical. However, puncture size and setal length do not seem to be related to each other or the ability of a species to retain pollen. Whether these factors contributed to a wasp's ability to accumulate pollen was not considered here.

Although poorly represented in collections, pairs that had remained *in copula* after collection had little pollen attached to their bodies. Those that were examined also had some pollen on the top of second abdominal segment (metasomal tergite 1), although this may be coincidental. Given that mating pairs feed extensively on nectar, it seems likely that the paucity of pollen grains is an artefact of the pinning process.

Representative specimens of all the genera listed in Table 1 had pollen on the body, as did most of the remaining genera: *Aeolothynnus, Ariphron, Chilothynnus, Gymnothynnus, Leiothynnus, Nitidothynnus, Pentazeleboria, Tachynoides, Tachyphron* and *Thynnus.* Several genera had little pollen. Those genera with a concave head (i.e. *Tachynomyia,*

Figure 1. Mating pair of flower wasps *Zaspilothynnus nigripes* at inflorescence of *Hakea trifurcata* (Proteaceae) with the winged male (above) covered in pollen and feeding the female by regurgitating nectar. North of Badgingarra, southern Western Australia. (Keith Smith)

Figure 2. Same mating pair of *Zaspilothynnus nigripes* as shown in Figure 1 with the wingless female (below) feeding on nectar. North of Badgingarra, southern Western Australia. (Keith Smith)

Tachynoides and *Tachyphron*) tended to have very little pollen, most of which was behind the top of the head and on the front of the thorax. *Gymnothynnus*, which has a strongly punctate head and thorax, tended to have dirt rather than pollen on the body; and *Nitidothynnus*, which has a smooth head and body, had no pollen. This may be an indication that a smooth body does not retain pollen for any length of time. No pollen was found on *Bifidothynnus* or *Dythynnus*, but most specimens of *Dythynnus* had an unknown white residue on their bodies.

Discussion

Despite the prominence of flower wasps in the Australian wasp fauna, and the abundance of specimens in museums collections, there are relatively few host plants documented. This introductory paper confirms that flower wasps are found on Myrtaceae more often than other families, but that they also utilise other plant families. Notably, several diverse groups in the Australian flora have been rarely or never recorded as food plants (e.g. Asteraceae, Ericaceae). Most records are from Myrtaceae that typically have open-faced flowers that permit easy access to nectar. Outside the Myrtaceae, the only plant genus where a wide range of genera has been recorded is *Hakea* (Proteaceae). Several species of *Hakea*, such as *H. trifurcata*, often attract large numbers of mating pairs (Phillips *et al.* 2009). In southwestern Australia, some genera of flower wasps are commonly seen on *Xanthorrhoea* (Phillips *et al.* 2009). Outside of these groups, records of thynnines foraging on nectar or pollen are relatively infrequent. However, systematic collection of pollinators is required to more accurately determine the extent to which this trend occurs due to a bias in collecting, arising from geographical and taxonomic variation in collection effort.

The prevalence of thynnines as floral visitors to some plant genera, in particular *Chamelaucium*, *Leptospermum* and *Hakea*, raises the possibility that some plant species may have undergone adaptations towards pollination by flower wasps. Increasing the attractiveness of a plant to flower wasps is most likely to take the form of a floral structure that increases their foraging efficiency, or tailoring the nectar reward to the preference of thynnines (e.g. Shuttleworth & Johnson 2009). An understanding of floral adaptations to pollination by flower wasps may aid in understanding why these wasps appear to show strong preferences towards certain plant genera.

Interestingly, some abundant genera of flower wasps, such as *Neozeleboria* and *Phymatothynnus*, are relatively rarely observed foraging on nectar. Similarly, in some habitats in southern Australia that support a high density of these wasps, it is very rare to see them foraging on nectar. These observations raise the possibility that in some genera, and in some environments, flower wasps might switch from using nectar plants to other food sources such as the exudates of other insects. These possibilities need to be evaluated by combining pollen swabbing (e.g. Menz *et al.* 2013) with detailed observations of the behaviour of pollinators.

Morphology of the pollinators in relation to diet

The morphology of the male may be relevant to how often flower wasps feed. In males of *Tachynomyia, Tachyphron* and *Tachynoides* (and also the New Guinean genera *Deuterothynnus* and *Heligmothynnus*) the head is strongly concave posteriorly and margined with long setae. This concavity is capable of retaining a large volume of liquid (presumably nectar which, when retained in preserved pinned specimens, dries to a small, pale mass). This liquid was found by Given (1953) to be used by male *Tachynomyia* to feed a female during courtship and coupling. Whether this is the only use is unknown. This structure may enable these genera to collect nectar faster by capillary action and may act as a food reserve so that wasps visit flowers less often and move longer distances between food plants or between breeding and feeding sites (e.g. Ridsdill Smith 1970b).

Interestingly, different species of male flower wasps show considerable variation in the shape and size of their mouthparts. The mouthparts tend to be longer in those species that have an enlarged clypeus, which may represent a specialisation for smaller wasps to use deeper flowers. While in many members of the Myrtaceae the nectar is presented on the relatively open-faced flower, it would be of interest to test if there is an association between mouthpart morphologies and those species that frequently feed on tubular flowered species.

The absence of pollen on the limited number of known specimens of *Bifidothynnus* may be a reflection of the small sample size, but this genus is so distinct morphologically (most obviously in the male genitalia and wing venation and the female terminalia) from all other flower wasps that there may be corresponding differences in its biology that are yet to be observed. Similarly, *Dythynnus* lacked pollen on the body of all specimens examined. Most individuals did however, have traces of an unidentified white residue. This may be remnants of hemipteran exudates or other non-floral food.

Conclusions and future directions

While this study has supported the conclusion that members of the Myrtaceae tend to be the main food plants of flower wasps, it also highlights how little is known about other food sources. In this context, studies of alternative food sources will be important for not only understanding the ecological requirements of pollinators and their susceptibility to landscape modification, but also for resolving how such diverse communities of thynnines co-exist with apparently similar diets. Resolving these issues will require systematic studies of the diet and behaviour of flower wasps. Such work will be important for not only understanding the biology of a diverse group of insects, but understanding their role in the pollination of a large number of Australian plant species.

Acknowledgements

Fieldwork of RDP was supported by grants from the Australian Orchid Foundation, the Holsworth Wildlife Research Endowment and the School of Plant Biology at the University of Western Australia. The authors acknowledge and appreciate the use of the two photos taken by Keith Smith.

References

Alcock J. (1981) Notes on the reproductive behaviour of some Australian thynnine wasps (Hymenoptera: Tiphiidae). *Journal of the Kansas Entomological Society* 54, 681–693.

Alcock J. and Gwynne D.T. (1987) Courtship feeding and mate choice in thynnine wasps (Hymenoptera: Tiphiidae). *Australian Journal of Zoology* 35, 451–548.

Bernhardt P. (1987) A comparison of the diversity, density and foraging behaviour of bees and wasps on Australian *Acacia*. *Annals of the Missouri Botanical Garden* 74, 42–50.

Bridwell J.C. (1917) Notes on the Thynnidae. *Proceedings of the Hawaiian Entomological Society* 3, 263–265.

Brothers D.J. (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *University of Kansas Science Bulletin* 50, 483–648.

Brothers D.J. and Carpenter J.M. (1993) Phylogeny of Aculeata: Chrysidoidea and Vespoidea. *Journal of Hymenoptera Research* 2, 227–304.

Brown E.M., Burbidge A.H., Dell J. *et al.* (1997) *Pollination in Western Australia: A database of animals visiting flowers*, Handbook No. 15. Western Australia Naturalists' Club, Perth.

Burrell R.W. (1935) Notes on the habits of certain Australian Thynnidae. *New York Entomological Society Journal* 43, 19–29.

Campbell A.J. & Brown G.R. (1994) Distribution of parasites of scarabs (Coleoptera: Scarabaeidae) in relation to remnant vegetation: a preliminary analysis. *Memoirs of the Queensland Museum* 36, 27–32.

Campbell, A.J. and Brown, G.R. (1998) Biological control of scarabs causing eucalyptus dieback. A report for the Rural Industries Research and Development Corporation. RIRDC, Barton. RIRDC Publication 98/3, 1/32.

Froggatt W.W. (1907) *Australian Insects*. William Brooks and Co., Sydney.

Given B.B. (1953) General report on a search for parasites of Melolonthinae in Australia. *New Zealand Journal of Science and Technology* (B) 34, 322–340.

Given B.B. (1957) Observations on behaviour of Australian Thynninae. Proceedings of the 8th Science Congress, Manila 3A, 1265–1274.

Goodacre W.A. (1947) *The honey and pollen flora of New South Wales*. NSW Government Printer, Sydney.

Illingworth J.F. (1921) Natural enemies of sugar-cane beetles in Queensland. *Bureau of sugar experiment stations Division of entomology Bulletin* 13, 1–47.

Menz M.H.M., Phillips R.D., Dixon K.W. *et al.* (2013) Mate-searching behaviour of common and rare wasps and the implications for pollen movement of the sexually deceptive orchids they pollinate. *PLoS ONE*, 8(3): e59111. doi:10.1371/journal.pone.0059111 (accessed 20 October 2013)

Naumann I.D. (1993) *CSIRO handbook of Australian insect names. Common and scientific names for insects and allied organisms of economic and environmental importance* (6th edition). CSIRO, East Melbourne.

Pate V.S.L. (1947) A conspectus of the Tiphiidae with particular reference to the Nearctic forms. *Journal of the New York Entomological Society* 55, 115–143.

Peakall R. (1990) Responses of male *Zaspilothynnus trilobatus* Turner wasps to females and the sexually deceptive orchid it pollinates. *Functional Ecology* 4, 159–167.

Peakall R., Ebert D., Poldy J. *et al.* (2010) Pollinator specificity, floral odour chemistry and the phylogeny of Australian sexually deceptive *Chiloglottis* orchids: implications for pollinator-driven speciation. *New Phytologist* 188, 437–450.

Phillips R.D., Brown A.P., Dixon K.W. and Hopper S.D. (2011) Orchid biogeography and the factors associated with rarity in a biodiversity hotspot: the Southwest Australian Floristic Region. *Journal of Biogeography* 38, 487–501.

Phillips R.D., Faast R., Bower C.C. *et al.* (2009) Implications of pollination by food and sexual deception for pollinator specificity, fruit set, population genetics and conservation of *Caladenia* (Orchidaceae). *Australian Journal of Botany* 57, 287–306.

Pilgrim E.M., von Dohlen C. and Pitts J.P. (2008) Molecular phylogenetics of Vespoidea indicate paraphyly of the superfamily and novel relationships of its component families and subfamilies. *Zoologica Scripta* 37, 1–22.

Rayment T. (1935) *A Cluster of Bees.* Endeavour Press, Sydney.

Ridsdill Smith T.J. (1970a) The biology of *Hemithynnus hyalinatus* (Hymenoptera: Tiphiidae), a parasite on scarabaeid larvae. *Journal of the Australian Entomological Society* 9, 183–195.

Ridsdill Smith T.J. (1970b) The behaviour of *Hemithynnus hyalinatus* (Hymenoptera: Tiphiidae), with notes on some other Thynninae. *Journal of the Australian Entomological Society* 9, 196–208.

Ridsdill Smith T.J. (1971) Field notes on the occurrence of *Hemithynnus hyalinatus* (Hymenoptera: Tiphiidae) as a parasite of scarabaeids on the New England Tablelands. *Journal of the Australian Entomological Society* 10, 265–270.

Salter K.E.W. (1963) Revision of the Thynnidae. Part V. A contribution towards a knowledge of the Thynnidae of The Philippines, Indonesia, New Guinea, The Solomons, New Caledonia and Lord Howe Island. *Proceedings of the Linnean Society of New South Wales* 87, 223–266.

Salter K.E.W. (1967) Studies on Australian Thynnidae. VI. A review of investigations on the Thynnidae of Australia. *Journal of the Entomological Society of Australia (New South Wales)* 3, 39–43.

Schiestl F.P. (2004) Floral evolution and pollinator mate choice in a sexually deceptive orchid. *Journal of Evolutionary Biology* 17: 67-75.

Shuttleworth A. and Johnson, S.D. (2009) The importance of scent and nectar filters in a specialized wasp-pollination system. *Functional Ecology* 23, 931–940.

Tillyard R.J. (1926) *Insects of Australia and New Zealand.* Angus and Robertson, Sydney.

Turner R.E. (1914) New fossorial Hymenoptera from Australia and Tasmania. *Proceedings of the Linnean Society of New South Wales* 38, 608–623.

Williams F.X. (1919) A note on the habits of *Epactiothynnus opaciventris* Turner, an Australian Thynnid wasp. *Psyche* 26, 160–162.